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DEVELOPMENT AND METAMORPHOSIS OF THE BRITTLE STAR *OPHIOCOMA PUMILA*: EVOLUTIONARY AND ECOLOGICAL IMPLICATIONS[1]

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Abstract

The development to metamorphosis of the shallow-water tropical-Atlantic ophiuroid *Ophiocoma pumila* is described for the first time. This species possesses an eight-armed planktotrophic ophiopluteus larva that has a potential pelagic existence of three months (26–27.5°C), considerably longer than other brittle star species so far studied. This likely accounts for the amphi-Atlantic distribution of *O. pumila*. During metamorphosis, all of the larval arms are resorbed into the developing ophiuroid rudiment although the right antero-lateral arm disappears last. The metamorphosing larva transforms into a highly mobile vitellaria possessing transverse ciliary bands and tube feet. Ophiuroid vitellariae have hitherto been described only for species with abbreviated lecithotrophic development. The vitellaria of *O. pumila* can delay settlement for at least a week and probably functions as a pre-settling exploratory stage. The discovery of both an ophiopluteus and a vitellaria in the ontogeny of a brittle star strongly supports the proposal that ophiuroid vitellariae are related to ophioplutei and are not a divergent larval series. Abbreviated development in brittle stars with vitellariae may be the outcome of heterochrony caused by an acceleration of metamorphosis. Little is known about ophiuroid metamorphosis so it is possible that the ophioplutei of many other species pass through a vitellaria stage towards the end of their pelagic existence.

Introduction

> The fact that in several forms, especially those which keep one of the anterolateral arms intact during metamorphosis, the ciliated band is broken up in pieces, so as to recall the ciliated rings in the Auricularian pupa, may merely be hinted at here. The discussion of its meaning must be left for another occasion.
>
> Mortensen, 1921, p. 125

Many ophiuroid echinoderms have a feeding (planktotrophic) larva, the ophiopluteus, which usually possesses four pairs of arms supported by skeletal spicules and bordered externally by a ciliated band. Ophioplutei generally have a planktonic existence of about one month or less (Hendler, 1975) followed by a relatively gradual metamorphosis that commences prior to settlement (Chia and Burke, 1978; Strathmann, 1978). Two basic patterns of metamorphosis are presently known (Mortensen, 1921, 1931). In the first (here called Type I) as exemplified by *Ophiothrix* spp., *Ophiomaza cacaotica*, and *Ophiopholis aculeata* (MacBride, 1907; Mortensen, 1937, 1938; Olsen, 1942; Mladenov, 1979), three pairs of shorter, inner

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arms are simultaneously resorbed into the developing ophiuroid rudiment while an outer pair of longer postero-lateral arms remains intact. The rudiment quickly develops tube feet and becomes suspended, oral surface downwards, from the postero-lateral arms. This form probably functions as a pre-settling exploratory stage with the ciliated postero-lateral arms used for swimming and maneuvering and the tube-feet for substrate testing and attachment.

A second type of ophiuroid metamorphosis (here called Type II) has been described only superficially for ophioplutei of *Amphiura filiformis* and *Ophiura albida* (Mortensen, 1931), and for several unidentified ophioplutei collected from the plankton during metamorphosis (Mortensen, 1921). In these, all four pairs of larval arms are resorbed into the rudiment, although the right antero-lateral arm apparently disappears last. Mortensen (1921) made the interesting but little known observation that during the metamorphosis of some of these larvae the ciliated band associated with the shrinking arms appears to become discontinuous, forming rings around the developing rudiment. The rudiment then resembles, in Mortensen's words, an auricularian pupa (= holothurian doliolaria; see Mortensen, 1927, p. 355). No one has yet verified this observation nor speculated on its possible evolutionary and functional significance.

Strathmann (1978) recognized that the timing of metamorphosis relative to settlement in brittle stars with Type II metamorphosis is a conundrum which requires further study. Settlement could occur before the arms, with their band of cilia, are completely resorbed. If so, the larvae would retain some maneuverability at settlement (important, presumably, for site selection) but attachment structures (*i.e.,* tube feet) would not be fully developed. Alternatively, metamorphosis could be completed in the plankton with juveniles settling and attaching to the bottom. However, juveniles, because they lack a ciliated band, would have limited site selection capacity.

This paper reports that the ophiopluteus of the brittle star *Ophiocoma pumila* Lütken is potentially teleplanic and passes through a vitellaria (= doliolaria) stage during Type II metamorphosis. The evolutionary and ecological implications of these findings are considered.

Materials and Methods

Ophiocoma pumila were collected at a depth of 7 m from Columbus Park Reef (located on the west side of Discovery Bay, Jamaica) on the afternoon of 12 July 1982. At this site, *O. pumila* is abundant on and beneath the coralline red alga, *Amphiroa tribulis* (Ellis and Solander) Lamouroux. The brittle stars were taken to the nearby Discovery Bay Marine Laboratory and placed in fingerbowls containing sea water. Males and females spawned spontaneously at 1835 h on the same day. The fertilized eggs were rinsed several times with Millipore-filtered sea water and cultured in polystyrene dishes at 26–27.5°C (approximate temperature at the collecting site) in stirred Millipore-filtered sea water containing antibiotics (Mladenov, 1979). The resulting larvae were fed a mixture of the following algae: *Amphidinium carterae, Isochrysis galbana, Dunaliella salina, Phaeodactylum tricornutum,* and a Tahitian strain of *Isochrysis galbana.* The algal culturing procedures are outlined in Mladenov (1984).

On 30 July 1982 about 200 larvae were placed in a thermos with about 2 l of culture medium and transported to the Biology Department, Mount Allison University, Canada. Total transit time was 28 h. At Mount Allison the larvae were reared at 27°C as described above; the cultures were not stirred. The culture medium was prepared from Discovery Bay sea water which was also transported to Mount Allison.

Photographs were taken in transmitted light with a Zeiss compound microscope equipped with an Olympus OM-2n camera.

Results

Description of gametes

The spawned fertilized eggs of *Ophiocoma pumila* are approximately 73 μm in diameter (n = 7) and pink-red in color due to the presence of red pigment granules scattered throughout the cream colored ooplasm. Each egg is surrounded by a smooth fertilization envelope (Devaney, 1970). A single, clear polar body was usually visible beneath the fertilization envelope indicating that eggs are spawned and fertilized as secondary oocytes. Spermatozoa have spherical heads approximately 2.5 μm in diameter and tails approximately 40 μm in length (n = 5).

Larval development

A chronology of larval development for *O. pumila* is presented in Table I and a brief supplemental description is provided here.

Hatching from the fertilization envelope takes place at the early gastrula stage. Gastrulae are uniformly ciliated and possess a glycocalyx (= cuticle) which is easily resolved with the light microscope and which persists throughout larval development. The gastrulae swim just beneath the surface of the culture water; postero-lateral arm buds are evident two days after fertilization and by five days (Fig. 1A) the gastrulae have developed into feeding ophioplutei with postero-lateral arms and incipient antero-lateral arms. During the next eight weeks the ophioplutei slowly assume their final form, acquiring post-oral and postero-dorsal arms, and growing much larger in overall size. The fully formed ophiopluteus of *O. pumila* is a singularly beautiful larva characterized by a large pre-oral region; short, broad antero-lateral arms; and a pair of epaulettes. These are specialized regions of the ciliated band having longer cilia than the rest of the band and located at the base of the arms (Fig. 1B). The distance between the tips of the postero-lateral arms is approximately 1.1 mm. The skeleton is somewhat unusual because the body rods, which normally join in the

Table I

Chronology of larval development of Ophiocoma pumila *(26.0–27.5°C)*

Time	Developmental events
0	Spawning and fertilization.
3.5 h	Four-cell stage.
21 h	Gastrulae hatched from fertilization envelope.
1.5 days	Skeletal spicules are evident in gastrulae.
2.0 days	Postero-lateral arms begin to develop.
2.5 days	Digestive tract fully formed and feeding has begun as shown by the accumulation of phytoplankton cells in the stomach.
5.0 days	Antero-lateral arms begin to develop.
9.0 days	Post-oral arms begin to develop.
35 days	Postero-dorsal arms are evident.
61 days	Fully formed ophiopluteus larva with four pairs of arms and a set of epaulettes.
79 days	First signs of metamorphosis: developing hydrocoel evident and arm resorption begins. Some ophioplutei delayed commencement of metamorphosis for at least 12 days.

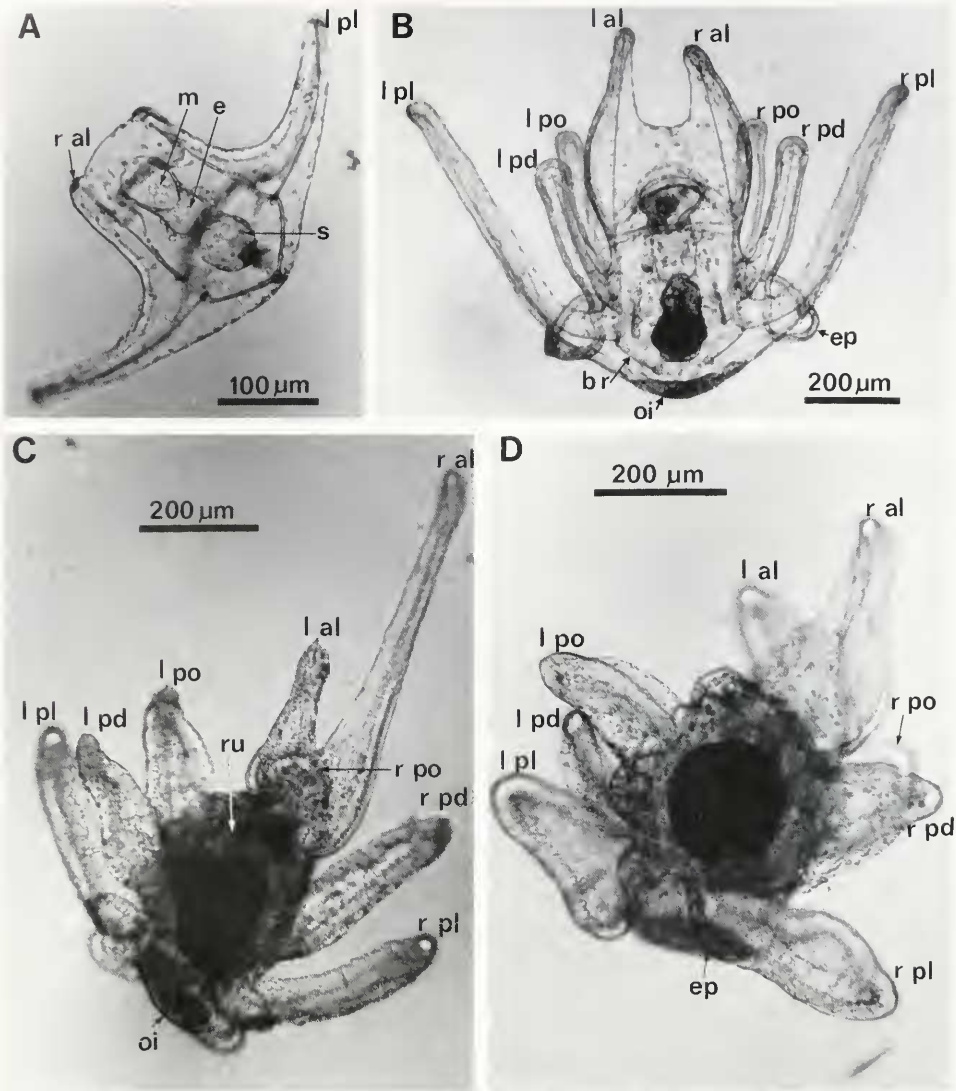

FIGURE 1. Larval and early metamorphic stages of *Ophiocoma pumila.* All photographs are of living material. A. Ventral view of a five-day-old ophiopluteus larva with well-developed postero-lateral arms, incipient antero-lateral arms, and a functional digestive tract. B. Dorsal view of a fully developed, 61-day-old ophiopluteus larva; note the epaulettes at the base of the postero-lateral arms, the rudimentary body rods, and the oily accumulation in the posterior end. C. Dorsal view of a 79-day-old larva in the early stages of metamorphosis; all arms, except for the right antero-lateral arm, are being resorbed into the ophiuroid rudiment; the right post-oral arm (which is visible beneath the antero-lateral arms) is bent across the ventral surface of the rudiment. D. A slightly later stage of metamorphosis (approximately 24 h after the commencement of arm resorption); note that the right antero-lateral arm has begun to be resorbed; the dark structure in the middle of the rudiment is the stomach. br, body rod; e, esophagus; ep, epaulette; l al, left antero-lateral arm; l pd, left postero-dorsal arm; l pl, left postero-lateral arm; l po, left post-oral arm; m, mouth; oi, oily accumulation; r al, right antero-lateral arm; r pd, right postero-dorsal arm; r pl, right postero-lateral arm; r po, right post-oral arm; ru, ophiuroid rudiment; s, stomach.

posterior end of the body of ophioplutei, become separated from one another by a gap during development (Fig. 1B). Furthermore, end and transverse rods, prominent at the posterior tip of each body rod in most ophioplutei, are very reduced in *O. pumila*. An unknown substance with an oily appearance accumulates within the posterior tip of the ophiopluteus during its development (Fig. 1B). Overall, the larva has a faint yellowish tint due to the presence of yellow-colored cells which are scattered throughout the epithelium but which are particularly noticeable in the region beneath the ciliary band.

Metamorphosis

The first indication of metamorphosis in *O. pumila* was the appearance of a 5-lobed hydrocoel on the left side of the oesophagus starting about 79 days after fertilization. Shortly afterwards, all of the larval arms, except for the right antero-lateral, begin to be resorbed slowly into the developing ophiuroid rudiment (Fig. 1C) (Table II). All arms are resorbed in place except for the right post-oral arm which is bent ventrally across the rudiment during resorption. The resorption of the right antero-lateral arm begins before the other arms are completely resorbed (Fig. 1D). The basal portion of this arm is still visible when the other arms have nearly disappeared (Fig. 2A). As each arm is resorbed, the internal skeletal rod appears to dissolve in proximal-distal fashion at about the same rate as the arm itself shortens. Two days after the commencement of arm resorption, the metamorphosing larva looks like a typical ophiuroid vitellaria (Fig. 2B). Vestiges of all the resorbed larval arms, except for the left antero-lateral arm, contribute to specific structures in the vitellaria: (1) the remains of the right antero-lateral arm form an anterior preoral lobe which has a ciliated band at its tip. (2) The right post-oral arm, which was bent ventrally during resorption, becomes a ciliated ridge positioned ventrally at the base of the preoral lobe. (3) A part of the ciliated band that was formerly associated with the right postero-dorsal arm becomes a ciliated band which is present interradially on the right ventral aspect of the vitellaria. (4) Similarly, the left post-oral and left postero-dorsal arms contribute to two bands of cilia, present in interradial positions on the left ventral surface of the vitellaria. (5) Tracts of cilia derived from the left and right postero-lateral arms form a ciliated band at the right posterior corner of the vitellaria. The oily accumulation within the posterior part of the ophiopluteus becomes incorporated into the posterior of the vitellaria. The ciliated epaulettes do not appear to contribute to any structures in the vitellaria. Note that clear vesicle-like structures develop at the tips of the remnants of the resorbed larval arms (see Fig. 2B). The significance of these structures is not known,

TABLE II

Chronology of metamorphosis of Ophiocoma pumila *(26.0–27.5°C)*

Time	Events
0	Arm resorption begins.
2 days	Arm resorption completed. There is now a vitellaria-type larva, with developing tube feet.
3 days	Tube feet are functional.
4 days	Vitellariae begin to settle. The ciliated bands are retained.
11 days	Preoral lobe has been resorbed and ciliated bands begin to disappear. The vitellaria has become a benthic juvenile.
25 days	Juvenile with five tiny arm buds.

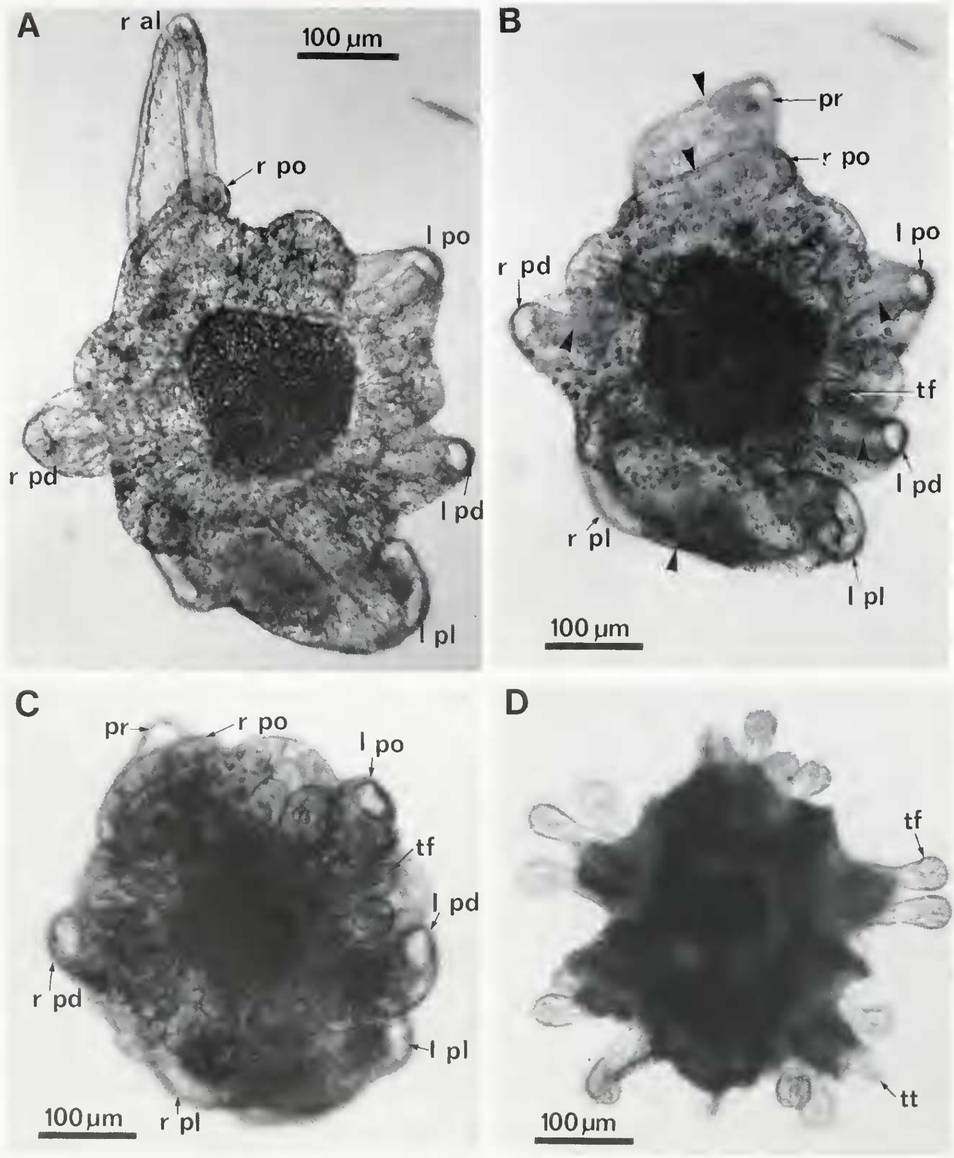

FIGURE 2. Late metamorphic, vitellaria, and juvenile stages of *Ophiocoma pumila*. All photographs are of living material. A. Ventral view of a late metamorphic stage (approximately 36 h after the commencement of arm resorption); note that all arms are nearly completely resorbed except for the right antero-lateral arm. B. Vitellaria (48 h after the commencement of arm resorption) showing the ophiuroid rudiment with developing tube feet, and the remains of the resorbed larval arms; the remnants of the right antero-lateral arm form the preoral lobe; the arrowheads indicate the position of ciliated bands. Note the clear vesicles at the tips of the larval arm remnants. C. An eight-day-old vitellaria; the ciliated bands are still present but the preoral lobe has shrunk considerably. D. Juvenile brittle star approximately three weeks after settlement; note the well-developed tube feet and the terminal tentacle evident at the tip of one of the developing arms. l pd, left postero-dorsal arm; l pl, left postero-lateral arm; l po, left post-oral arm; pr, preoral lobe; r al, right antero-lateral arm; r pd, right postero-dorsal arm; r pl, right postero-lateral arm; r po, right post-oral arm; tf, tube foot; tt, terminal tentacle.

but they may represent a by-product of arm resorption. The vitellaria possesses five pairs of tube feet, one pair per radius.

Although some ophioplutei in culture began to metamorphose 79 days after fertilization, some still had not begun metamorphosis at 91 days. This suggests that under natural circumstances delay of metamorphosis may occur.

The vitellariae of *O. pumila* are fast and maneuverable swimmers. In culture, they begin to settle four days after the commencement of metamorphosis, using the tube feet for attachment. However, vitellariae retain their ciliated bands for at least a week, during which time they can detach repeatedly from the substrate, swim about for a variable period of time, and then reattach and walk. The preoral lobe is gradually reabsorbed during this period (Fig. 2C). Then, the ciliated bands gradually disappear and the vitellaria becomes a benthic juvenile. The juvenile can move quickly over the bottom using the tube feet. If disturbed, it securely attaches itself to the bottom and is difficult to dislodge with a jet of water from a pipette. By roughly 25 days following the commencement of metamorphosis, the juvenile has 5 tiny arm buds, each with a small terminal tentacle at its tip (Fig. 2D).

Discussion

Comments on development within the genus Ophiocoma

In general, *Ophiocoma* ophioplutei are characterized by a large pre-oral region, short, broad antero-lateral arms, and well-developed epaulettes. However, discernible species-specific differences in shape, size, and coloration as well as in the structure and ontogeny of the body skeleton do exist (Grave, 1898; Mortensen, 1931, 1937). The *O. pumila* ophiopluteus is most similar in shape and size to that of *O. pica* from the Indo-Pacific. Furthermore, both have rudimentary body skeletons, the body rods being separated by a gap. In *O. pumila,* however, the body rods are joined at first (Fig. 1A) and then gradually separate as the ophiopluteus matures (Fig. 1B). In *O. pica,* on the other hand, the body rods are, apparently, never joined (Mortensen, 1937, p. 52). Devaney (1970) reported that in *O. pumila* the body rods were joined in this species. He did not rear the larvae long enough, though, to record the eventual separation of the body rods in the fully developed ophiopluteus. An oily accumulation, as observed in the larva of *O. pumila,* has not been reported or figured in other ophiocomid larvae.

Devaney (1970) separated *Ophiocoma* species into four groups on the basis of adult characters, with *O. pumila* and *O. pica* being placed into the PUMILA and PICA groups, respectively. The differences in the ontogeny of the body skeletons described here would seem to provide additional support for the separation of these two species. As Devaney (1970) suggested, more detailed studies of other premetamorphic characters might aid in the separation of *Ophiocoma* species into valid groups.

Evolutionary implications

At present, seven species of Ophiuroidea are known to possess a vitellaria larva: *Ophioderma brevispinum* (Brooks and Grave, 1899), *Ophionereis squamulosa* (Mortensen, 1921), *Ophiolepis cincta* (Mortensen, 1938), *Ophioderma longicaudum* (Fenaux, 1969), *Ophiolepis elegans* (Stancyk, 1973), *Ophioderma cinereum* (Hendler, 1979, p. 153) and *Ophionereis annulata* (Hendler, 1982). In all of these, development is abbreviated and the gastrula transforms directly into a vitellaria without passing through a pluteus stage.

The ophiuroid vitellaria would appear, at first analysis, to be fundamentally different from an ophiopluteus larva. The vitellaria is an armless, barrel-shaped, non-feeding larva with multiple transverse ciliary bands that are used solely for locomotion. The ophiopluteus, on the other hand, is an armed feeding larva with a single ciliated band which is used for both feeding and locomotion. It is not surprising then that several investigators (Hamann, 1901; Fell, 1945; Williams and Anderson, 1975) concluded that the vitellaria is evolutionarily distinct from the ophiopluteus. Mortensen (1921, p. 176), however, contended that the vitellaria was actually a reduced ophiopluteus. His argument was strengthened by his discovery of small calcareous structures in the vitellaria of *Ophiolepis cincta* (Mortensen, 1938) which he interpreted to be vestiges of an ophiopluteus skeleton. Still, this proposal remained questionable until Hendler (1982) presented persuasive evidence that certain skeletal spicules present in the vitellaria of *Ophionereis annulata* were indeed remnants of an ophiopluteus skeleton. Mortensen (1921) and later Hendler (1982) suggested that some ophioplutei have undergone a progressive reduction in number of arms and complexity of the skeleton thereby becoming vitellariae. The vitellaria is thus regarded as having evolved from an ophiopluteus form.

As shown in this paper, a vitellaria is the terminal stage in the larval ontogeny of *Ophiocoma pumila*. To be more precise, the vitellaria consists of the ophiuroid rudiment together with structural remnants of the ophiopluteus. There is great structural similarity between the *O. pumila* vitellaria and the vitellariae that have been described for species with abbreviated lecithotrophic development (Brooks and Grave, 1899; Mortensen, 1921, 1938; Fenaux, 1969; Stancyk, 1973; Hendler, 1982). Apart from the fact that all have a preoral lobe, similarities in pattern of ciliation are striking. Generally, lecithotrophic vitellariae possess a tuft of cilia at the tip of the preoral lobe, a band of cilia at the base of this lobe, three interradial tracts of cilia on the ventral aspect of the rudiment (two on the left side and one on the right side), and a band of cilia at the right posterior corner of the rudiment. The pattern of ciliation on the *O. pumila* vitellaria is identical. This strongly suggests that there is more than a superficial resemblance, and that the *O. pumila* vitellaria is homologous to the lecithotrophic vitellaria.

The discovery of both an ophiopluteus and a vitellaria in the ontogeny of a single species of brittle star implies an evolutionary affinity between brittle stars with an ophiopluteus larva and those with abbreviated development and a vitellaria larva. It also allows comment on the evolutionary mechanism linking the two forms. If the ontogeny of *O. pumila* is considered to be of an ancestral type, then the vitellaria could not have evolved from an ophiopluteus by reduction, since both ophiopluteus and vitellaria stages occur in the same life cycle. An alternative explanation is that the ophiopluteus has been lost from the life cycle whilst the vitellaria persists. This outcome might be the result of heterochrony, caused by an acceleration (see Gould, 1977) of metamorphosis such that it begins earlier and earlier in the ontogeny of descendants, thereby eclipsing the ophiopluteus stage altogether (Fig. 3). A similar argument was originally invoked by Fell (1945) (he labelled the process "recession of metamorphosis") to explain the abbreviated ophiopluteus larvae which form a continuous reduction series with fewer and fewer arms than normal. Fell's scheme is useful so long as it is recognized that the vitellaria is probably not the ultimate outcome of this reduction series but is, rather, a distinct stage which may have persisted through phylogeny despite reduction of the ophiopluteus itself.

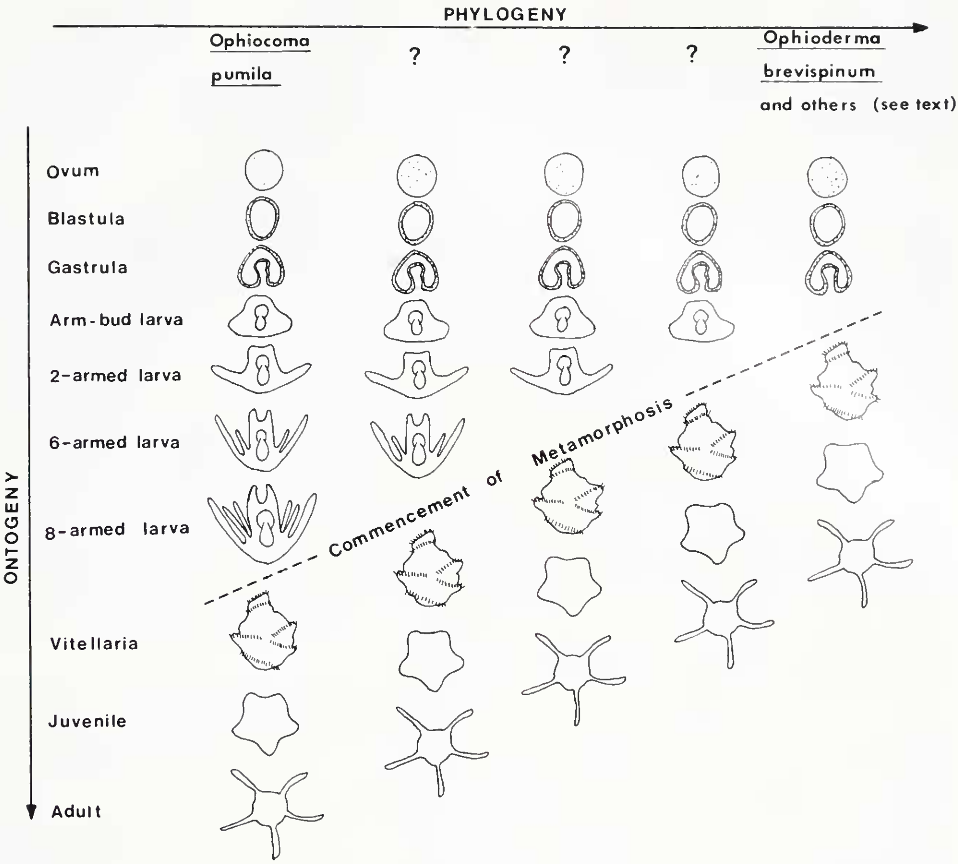

FIGURE 3. Diagram illustrating the outcome of a gradual acceleration of metamorphosis in a line of brittle stars with Type II metamorphosis. See text for further explanation.

The *O. pumila* life cycle is likely not unique among ophiuroids. It must be remembered that developmental information is available for only about 4% of the 2000 living ophiuroids and much of this is fragmentary, especially the details of metamorphosis (Hendler, 1975; pers. notes). Indeed, it is possible that a vitellaria exists in many or, perhaps, all species with a Type II metamorphosis.

The relationship between brittle stars with Type I and Type II metamorphosis is obscure. It is possible that brittle stars with Type I metamorphosis never possessed a vitellaria stage in their ontogeny and that their "suspended rudiment" stage serves the same function as the vitellaria (*i.e.*, pre-settlement exploration of the substrate; see next section). If so, Type I and Type II metamorphosis may be indicative of separate lines of larval evolution within the non-euryalinid brittle stars. Alternatively, it is possible that the vitellaria stage has been secondarily lost in this group and has been replaced by the "suspended rudiment" stage.

If acceleration of metamorphosis is a gradual process, as envisioned by Fell (1945), then further study should yield ophiuroids which have a reduced ophiopluteus (less than 8 arms) along with a Type II metamorphosis resulting in a vitellaria (Fig.

3). A vestigial ophiopluteus skeleton in some vitellariae, but not in others (Mortensen, 1921, 1938; Hendler, 1982) is likely a consequence of the extent of acceleration of metamorphosis *i.e.,* in some the skeleton starts to develop before the onset of metamorphosis; in others, metamorphosis takes place before the skeleton begins to develop.

Ecological implications

It is generally thought that ophioplutei have a relatively short pelagic existence (a month or less) and are incapable of long-distance transport in ocean currents (see Hendler, 1975). Although rate of development in laboratory culture is not necessarily indicative of what occurs in the ocean, it can be argued that *O. pumila* has the ability to survive in the plankton for up to three months and then metamorphose and settle normally. The larva of this species is thus potentially teleplanic and capable of long-distance dispersal. This may explain the wide geographic distribution of *O. pumila.* It has been recorded from insular and mainland regions of the Caribbean north to Bermuda and south to Brazil, and also from the west coast of Africa including the Azores, Gulf of Guinea, and Cape Verde Islands (Devaney, 1970). In fact, *O. pumila* is one of the few shallow-water ophiuroids with a tropical amphi-Atlantic distribution (Hyman, 1955). From Scheltema's (1977, Table 3) calculations, *O. pumila* larvae could be easily carried from the Gulf of Guinea to Brazil in the South Equatorial Current (60–154 days required) and occasional transport from Brazil to the Gulf of Guinea in the Equatorial Undercurrent may also take place (approximately 96 days required).

The *O. pumila* vitellaria, with its ciliated bands, which confer maneuverability, and its tube feet, which provide both temporary and final attachment, appear admirably adapted for pre-settlement exploration of the substrate. The ciliated bands remain for about a week providing the vitellaria with an extended opportunity to encounter a substrate suitable for the survival of the juvenile. The slowly shrinking preoral lobe, and the oily accumulation, probably sustain the vitellaria during this exploratory phase. Incidentally, the vitellariae resulting from abbreviated development in *Ophionereis squamulosa* and *Ophiolepis elegans* are also active swimmers and appear to "test" the substrate (Mortensen, 1921; Stancyk, 1973).

The question raised by Strathmann (1978) concerning the actual timing of settlement in brittle stars with Type II metamorphosis is resolved, at least for *O. pumila.* This species settles as neither an ophiopluteus nor a juvenile, but as a vitellaria. The vitellaria functions as the necessary intermediary between the pelagic and benthic phases of the life cycle. As mentioned previously, other species with Type II metamorphosis likely pass through a vitellaria phase as well.

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